International Journal of Primatology, Vol. 18, No. 3, 1997

The Pair-Bond Formation and Its Role in the Stimulation of Reproductive Function in Female Common Marmosets *(Callithrix jacchus)*

Hélderes Peregrino A. Silva[1,2] **and M. B. C. Sousa**[1]

Received May 6, 1996; accepted January 14, 1997

*The sociosexual relationship between male and female common marmosets (*Callithrix jacchus*) is characterized by pair-bond formation, which includes sexual and social interactions such as contact, huddling and allogrooming. The formation of heterosexual pairs in captivity sometimes is unsuccessful in terms of reproduction. We investigated the existence of a correlation between characteristics of sociosexual interaction of marmoset pairs and its role in stimulating reproductive function in females. We studied pair-bond formation during the first 10 weeks of pairing in eight unrelated heterosexual pairs of common marmosets (*Callithrix jacchus*) without prior sexual experience. In three of them, pregnancy occurred during the study period (group SR), and we compared the profile of their sociosexual interactions with that of the five other couples in which pregnancy was not registered (group NS) during that period. The results show differences between the two groups, related mainly to affiliative responses between male and female, with significantly higher levels of allogrooming and simultaneous piloerection in the SR group. Although we did not find significant differences in the frequency of mounting behavior between groups, their reproductive success was different, suggesting that some behavioral patterns related to cooperative interactions between the male and female could be expressing the pair-bond. These behaviors may be influencing the females' physiology and consequently successful reproduction in the species.*

KEY WORDS: *Callithrix jacchus*; reproductive success; pair-bond; social interactions.

[1]Setor de Psicobiologia, Departamento de Fisiologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, 59072-970, Natal, RN, Brasil.
[2]To whom correspondence should be addressed.

0164-0291/97/0600-0387$12.50/0 © 1997 Plenum Publishing Corporation

INTRODUCTION

In several primate species, the formation of the pair-bond is a key component of male and female reproductive strategies. However, the intensity, specific behavioral interactions, and duration of the pair-bond can vary widely, from occasional consortships to lifetime relationships.

The pair-bond in callitrichids is documented by captive and wild studies [captivity (Epple, 1977; Rothe, 1975; Kleiman, 1978; Hearn, 1978; Woodcock, 1982; Evans and Poole, 1983), wild (Soini, 1987; Ferrari and Lopes Ferrari, 1989; Digby, 1994)]. For males, the unequal operational sex ratio—with only one reproductive female in the majority of captive and wild observed groups—and, for females, the need for helpers to care for offspring seem to be the main immediate causes of the development of these exclusive relations.

In captivity, reproductive success for different pairs varies widely, whether in terms of the interval between initiation of pairing and first conception, length of the interbirth interval, or survival of offspring. There are various hypotheses to explain the differences in reproductive success between captive pairs. They implicate such characteristics as the level of experience of the male and the proximity of the female to dominant relatives (Evans and Poole, 1983), the sibling-rearing experience of the female (Tardif *et al.*, 1984), the age of the female and experience of the male (Tardif *et al.*, 1986), the level of environmental stress (Abbott and Hearn, 1978; Hearn, 1978; Johnson *et al.*, 1991), and the length of time that the female spent with her family group before being paired with a male (Kuderling, 1990).

Few studies of callitrichids focus on the effect of the pair-bond on reproductive success (Hearn, 1978; Evans and Poole, 1983). Although male participation in parental care has been emphasized by Ingram (1977), Cleveland and Snowdon (1984), and Arruda *et al.* (1986), male influence on reproductive function remains unclear. Moreover, we do not know what specific mechanisms could be responsible for this male influence or whether all males would be equally efficient in affecting female reproduction.

In an experiment with *Saguinus oedipus*, Widowski *et al.* (1990) clarified some aspects concerning the mechanisms of the stimulatory action of males on reproductive function in females. The stimulatory action of males was effective only when the male was unrelated to the female, and olfactory clues—pheromones—left by males were insufficient to initiate ovarian cycles in females. Accordingly, the authors concluded that other aspects—auditory, visual, or tactile clues—must also be involved in the stimulation of female reproductive function. These aspects are all components of social interactions between males and females.

The objective of our experiment was to determine if there is a relationship between characteristics of sociosexual interaction of male–female pairs of common marmosets and female reproductive function. The experiment charted the profile of these interactions starting at the initiation of pair formation.

MATERIALS AND METHODS

Eight unrelated heterosexual pairs of common marmosets (*Callithrix jacchus*) were the subjects. At the start of the experiment, the animals were young adults between 16 and 26 months-old (males) and 17 and 26 months old (females) (Table I). None of them were sexually experienced or had proven fertility. They were born at the Núcleo de Primatologia of the Universidade Federal do Rio Grande do Norte (UFRN) and lived with their family groups until the initiation of observations. We removed subjects from their families immediately before the beginning of the tests, and they did not have any contact—visual or olfactory—with their test partners before the tests. The compositions of the subjects' families were quite variable, ranging from two to six individuals when they were removed for the tests. They were housed in indoor/outdoor cages at the Núcleo de Primatologia at the UFRN. The cages are constructed of brick and wire screen and measure 2 × 1 × 1 m. We observed them via unidirectional window on the rear wall of the cages.

Experimental Procedure

The experimental procedure consisted of pairing tests in which the male was introduced into the female's cage for 30 min. We conducted tests between 0800 and 1100 three times per week for 10 weeks. Observations began when the male was placed in the female's cage and ended with him being transferred back to his own cage. We used continuous focal sampling method to record behaviors of both animals simultaneously, with frequency and duration of behaviors entered into a single notebook.

The behavioral categories are as follows.

Affiliative behavior includes duration of contact, proximity, allogrooming, and frequency of invitations for grooming, both successful and unsuccessful. We calculated Hinde's index (Hinde and Atkinson, 1970) from the frequency of approaches and retreats for the male and female. It indicates which subject was primarily responsible for initiating interactions at a given moment. A positive value indicates that the male was

Table I. Ages of the Subjects at the Time of Pairing, Social Condition of the Females in the Family Group, and Week after Pairing in Which Conception Occurred in the Eight Pairs

Pair	Age (mo)		Family composition	Conception
1			Mother/father, twin male	
Male	183	16		8th wk
Female	172	19		
2			Mother/father	10th wk
Male	95	19		
Female	128	17		
3			Mother/father, one set of younger siblings	No
Male	107	28		
Female	132	20		
4			Mother/stepfather at 13 mo	No
Male	153	30		
Female	170	23		
5			Mother/stepfather at 10 mo, twin male,	No
Male	201	30	two sets of younger siblings	
Female	222	20		
6			Mother/stepfather at 7 mo, two sets of	20th wk
Male	223	25	younger siblings	
Female	232	22		
7			Mother/father, twin male, two sets of	No
Male	207	26	younger siblings	
Female	268	26		
8			Mother/father, twin female, two sets of	No
Male	229	30	younger siblings	
Female	262	26		

primarily responsible, while a negative value indicates that the female was responsible.

Sexual behavior includes frequency of copulation attempts and successes and mounting refusals. Copulation is successful when microscopic examination shows spermatozoa in the vaginal fluid collected from the female immediately after each test in which copulation occurred. The mounting refusals by females occurred when they assumed positions that prevented male mounts or when they showed agonistic behaviors toward the males when they attempted to copulate.

Coordinated pair behavior is the frequency of simultaneous piloerection. The details for each behavioral category follow the definitions of

Stevenson and Poole (1976), Poole (1978), and Kendrick and Dixson (1984).

Statistical Analysis

We calculated the date of probable conception retroactively by taking the date of the birth of offspring and subtracting 144 days, which is the approximate gestation period for *C. jacchus* (Hearn, 1983). Conception occurred during the first 10 weeks after pairing—between week 8 and week 10—for two of the eight pairs and also during the 20th week for another pair. We sorted the eight pairs into two groups in order to compare behavioral profiles: Group RS ($N = 3$) includes three pairs in which the female conceived within 20 weeks after the beginning of the study period, while Group NS ($N = 5$) is the remaining five pairs in which conception did not occur during this period. We used nonparametric tests (Siegel, 1975) for statistical analysis due to the small size of the sample. We employed the Kruskal-Wallis test for comparison between groups and Spearman's coefficient to verify the occurrence of correlation between behavioral categories. Significance is ≤ 0.05.

RESULTS

Both groups presented similar profiles with respect to the affiliative behaviors of contact and proximity ($p > 0.05$). Contact behavior presented an irregular profile with a tendency to increase in the last week of observation. Proximity behavior had a more constant profile during the 10 weeks (Fig. 1A). The weekly average for contact behavior is 75.8 ± 15.0 sec for the RS group and 177.6 ± 31.5 sec for the NS group, and the average duration of proximity is 88.2 ± 8.5 sec for the RS group and 138.7 ± 10.9 sec for the NS group.

The females in the RS group approached males significantly more than females in the NS group did (Kruskal-Wallis test, $k = 41.26$, $p < 0.01$). These differences were evident in values of Hinde's index, which show that in the RS group, females were more involved in initiating interactions than in the NS group, in which males were primarily responsible for initiating interactions throughout the study (Fig. 1B).

With respect to allogrooming behavior, there is a significant difference between groups in the duration of grooming by males (Fig. 2A). It was much greater for males in the RS group (351.9 ± 53.5 sec; $k = 26.21$, $p < 0.01$). In the NS group, the time spent in allogrooming by males (95.8

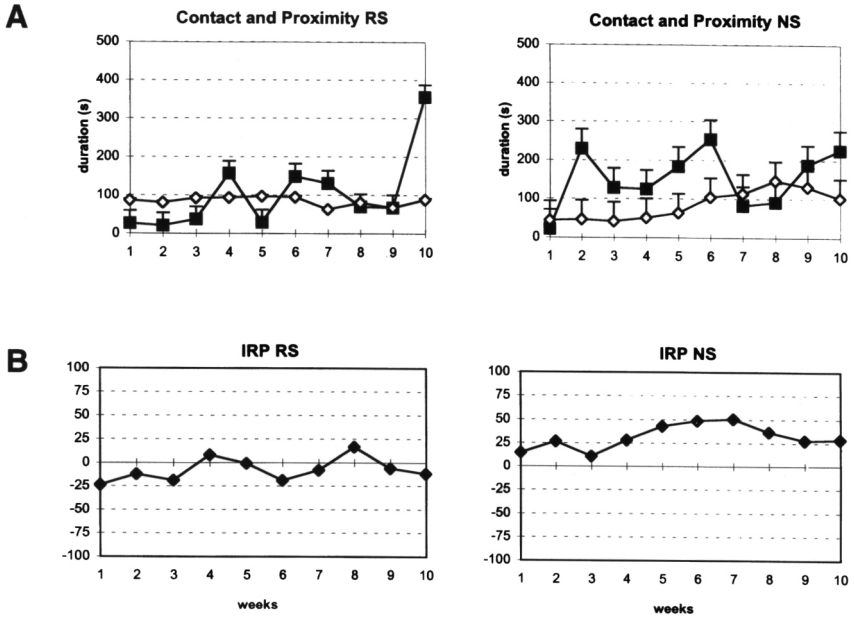

Fig. 1. Weekly mean duration (+SE) of contact (■) and proximity (◊) behaviors (A) and Hinde's index (B) in the RS (conception occurring during the first 20 weeks after pairing) and NS (no successful reproduction) groups.

± 2.3 sec) remained low throughout the first 6 weeks of observation, increased in the seventh week, but returned almost to zero in the last week of observation. In addition, the frequency of successful grooming invitations by females in the RS group is significantly higher than in the NS group ($k = 41.81, p < 0.01$). Females in this group succeeded in soliciting grooming an average of 76% of the time, while females in the NS group had an average success rate of only 43%.

For both groups, allogrooming by females did not begin until the third week of observation. This behavior is significantly greater in females from the RS group (51.8 ± 13.9 sec) compared to the NS group (13.25 ± 5.6 sec; $k = 10.47, p < 0.01$) (Fig. 2B). The difference between groups in the frequency of successful grooming invitations by males is not statistically significant. In the RS group, males were successful in soliciting grooming 21% of the time, while in the NS group males averaged 28% success.

In the RS group, significant positive correlation exists between (1) the frequency of grooming solicitation by females and the time spent allogrooming by males (Spearman's correlation coefficient, $r_s = 0.84, p < 0.01$) and (2) the frequency of invitations by males and the time spent al-

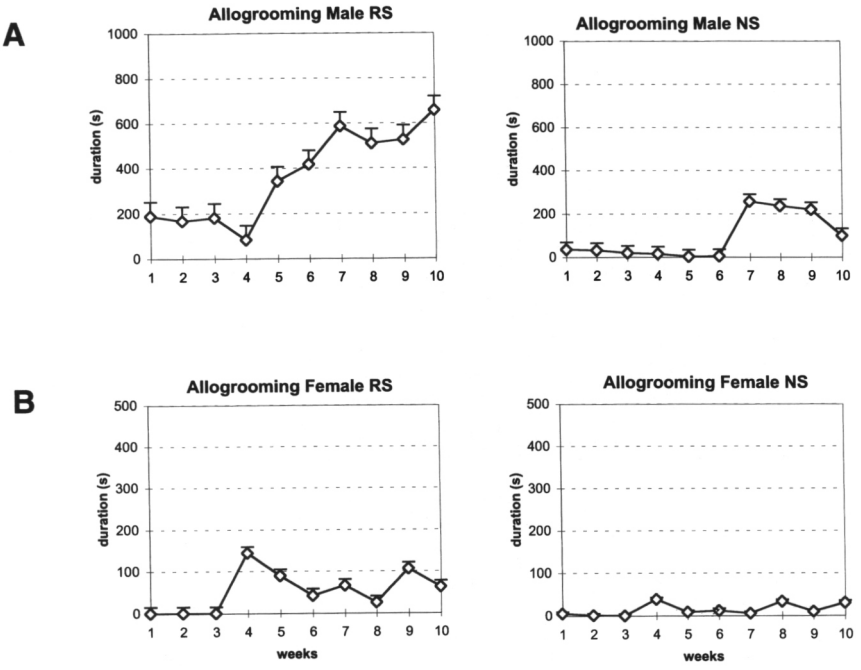

Fig. 2. Weekly mean (+SE) duration of allogrooming behavior to males (A) and females (B) in the RS (conception occurring during the first 20 weeks after pairing) and NS (no successful reproduction) groups.

logrooming by females ($r_s = 0.53$, $p < 0.02$). The frequency of invitations of females and males covaried ($r_s = 0.53$, $p < 0.05$). None of these behavioral relationships occurred in the NS group.

With respect to sexual behavior, females from the RS group were more attractive to the males, concerning the frequency of mounting attempts, which is significantly higher in the RS group ($k = 23.5$, $p < 0.01$) (Fig. 3A). However, males in this group approached females less than males approached females in the NS group. There is no significant difference in the frequency of successful copulation between groups. In fact, in spite of the short-term conceptions that occurred in females in the RS group, the percentage average frequency of successful copulation is higher in the NS group (43%) than in the RS group (30%) (Fig. 3B). Females in the RS group were more receptive than those in the NS group. This was evidenced by the significantly lower frequency of mounting refusals by females in the RS group ($k = 4.2$, $p < 0.01$) (Fig. 3C).

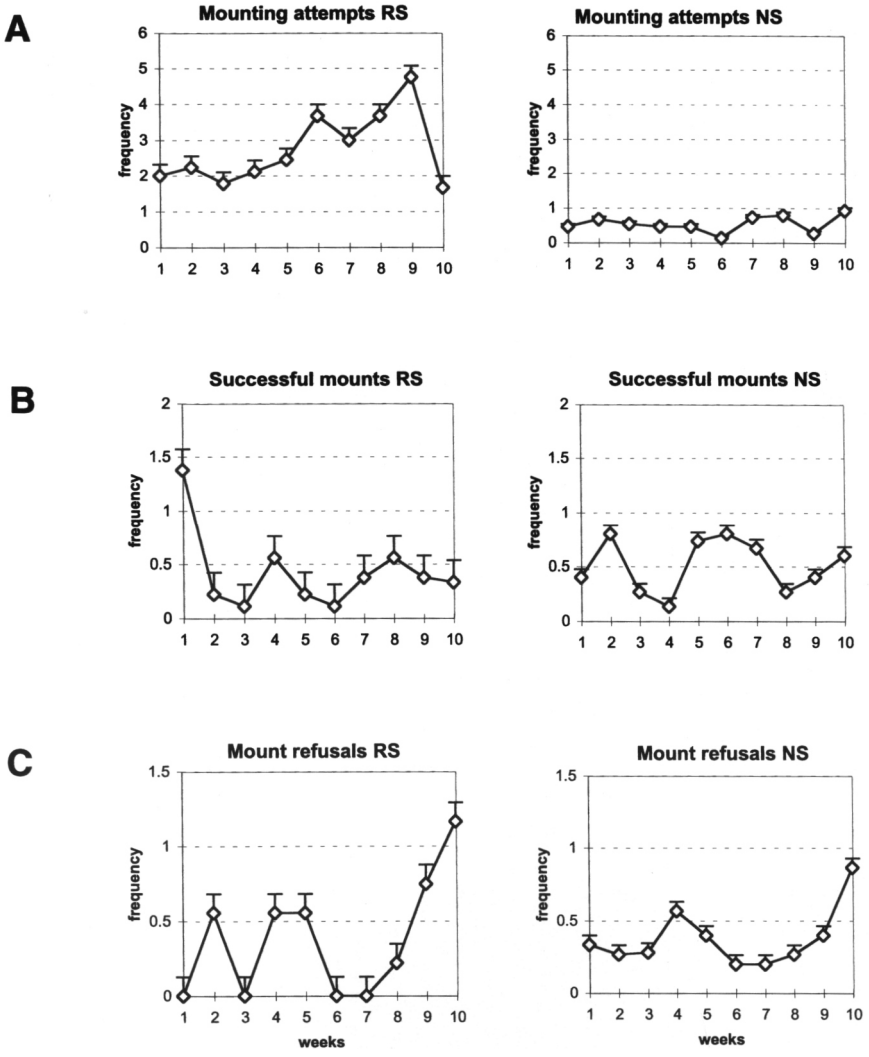

Fig. 3. Weekly mean frequency (+SE) of sexual behaviors, (A) Male mounting attempts, (B) male successful mounts, and (C) female mounting refusals, in the RS (conception occurring during the first 20 weeks after pairing) and NS (no successful reproduction) groups.

The frequency of simultaneous piloerection behavior is significantly higher in the RS group ($k = 13.8$, $p < 0.01$; mean ± SE, 1.6 ± 0.1 per week) than in the NS group (0.17 ± 0.1) (Fig. 4). In group RS, the behavior

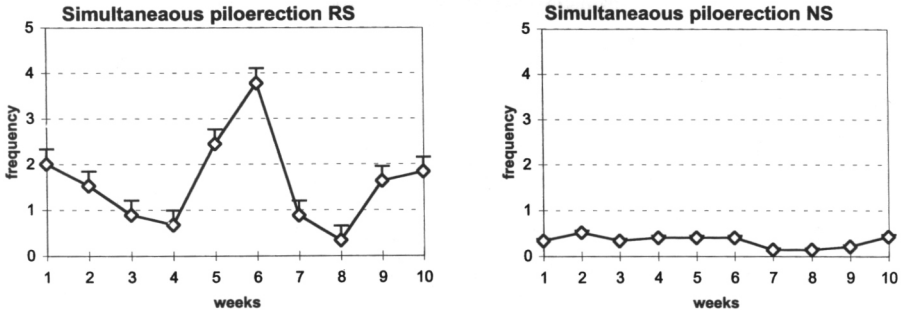

Fig. 4. Weekly mean frequency (+SE) of simultaneous piloerection behavior in the RS (conception occurring during the first 20 weeks after pairing) (A) and NS (no successful reproduction) (B) groups.

of simultaneous piloerection and the frequency of mounting attempts reached a peak during the sixth week. In this group, the frequency of mounting attempts is significantly correlated with the frequency of simultaneous piloerection ($r_s = 0.51$, $p < 0.05$). The frequency of approaches by females in the RS group is also significantly correlated with the frequency per week of simultaneous piloerection ($r_s = 0.53$, $p < 0.02$) and with the frequency of mounting attempts ($r_s = 0.52$, $p < 0.05$).

DISCUSSION

Our results show a significant difference in sociosexual interactions between the two groups. Separation of the animals except during the pairing tests proved extremely useful since social deprivation enhanced sexual response of the animals (Snowdon, 1990; Ziegler *et al.*, 1993). It allowed us to measure behavioral categories such as mounting refusal, which is a strong indicator of female receptivity. Under permanent pairing conditions, this would be a very rare behavior. In the short-term reproductively successful pairs (RS group), the females were more receptive to the males than were the females in the NS group, which conception did not occur. Furthermore, the females of the RS group showed greater interest in males, promoting proximity during 7 of 10 weeks of pairing tests. The occurrence of ovulation was confirmed by the fact that these females were able to conceive within the first 20 weeks after pairing. Although measurements for hormonal monitoring was not available, these data suggest that females in the NS group might not have ovulated during this study period or had had early miscarriage. Although the high quantities of motile spermatozoa

observed by microscopic analysis of the vaginal flux of females did not alone indicate normal fertility for the males, this finding confirmed the successful copulation in this group and the probability that females were not ovulating.

The absence of reproduction in NS pairs demonstrates that females can react differently in social and reproductive terms to the presence of males, since the major differences observed between males of the two groups were not associated with the effectiveness of copulation. As all female subjects were daughters living in their natal groups until the beginning of the pairing tests, the differences may also indicate that the reproductive condition of females was not equal for both groups before the pairing tests. In a study of behavioral and social correlates of escape from suppression of fertility and sexual behavior in common marmoset daughters living in their family groups, Saltzman *et al.* (1997b) observed that 46.3% of daughters ovulated at least once and this value increased up to 87.5% when the father had been replaced by an unfamiliar adult male. As with the introduction of a new male in the family group, the absence of the mother also stimulated the fertility of the dominant sisters in cotton-top tamarins [*Saguinus oedipus* (Heistermann *et al.*, 1989)]. In our study, all the mothers were in the group, and five of the eight females were living with their natural fathers, whereas three were with stepfathers. However, of the three females that became pregnant, two were living with fathers. This indicates that besides the prior condition in the family group, the presence of a new unrelated male exerts an additional influence on the reproductive success of young adult female marmosets. The stimulating role of pairing an unrelated male upon the onset of ovulation in callitrichid adult females is well documented [*Callithrix jacchus* (Abbott and George, 1991), *Saguinus oedipus* (Widowski *et al.*, 1990)]. Recently, Saltzman (1997b) extended this observation by demonstrating that even in the presence of the mother, the incorporation of a new male into the family group could stimulate both ovulation and sexual behavior in adult daughters. Although the introduction of the stepfathers in our family groups occurred when the females were juveniles, we registered episodes of aggressive interactions between the mother and the oldest daughter at the time of introduction (female 170; 13 months).

The most important findings of this work was that the affiliative interactions between the male and the female from the two groups were different. In particular, the duration of grooming the female was significantly greater among males from the RS group. The males in this group, besides spending more time grooming females, were also more responsive to grooming solicitations by females. Females in the RS group were significantly more successful in soliciting grooming by males than were females

in NS group. The majority of studies concerning social interaction between recently paired callitrichids has shown more allogrooming by males than by females (Woodcock, 1982; Evans and Poole, 1983; Savage *et al.*, 1988). This has also been shown in established pairs (Rothe, 1975; Poole, 1978). Kleiman (1977) even suggested that this aspect of interaction between the pair could be generalized as a characteristic of the monogamous relationship in primates. The opposite is generally found in polygynous species, in which females tend to groom males more than they are groomed by them. However, prior studies on bonds between members of callitrichid pairs have shown that this distribution is not the rule in all pairs of species that have been studied. Time spent in allogrooming by males and females often varies in relation to the degree of investment in the relationship and with the reproductive status of the female (Price, 1992). Considering time spent in allogrooming as an indicator of the investment in the strength of the relationship, the males in RS group presented higher levels of investment than the males in NS group. These could be occurring because the callitrichid males can identify the reproductive condition of the female by behavioral or olfactory cues or both (Kendrick and Dixson, 1983; Ziegler *et al.*, 1993).

Simultaneous piloerection is another behavior that was significantly different between the two groups. Although we can not disregard the possibility that it could be influenced by the ovarian functioning of the females before pairing (in natal groups) as demonstrated by Saltzman *et al.* (1997a), wherein cycling daughters bristle-strutted significantly more often than acycling daughters did, this behavior performed together with the mate appears to have multiple functions in inter- and intragroup communication, both related to contexts of agonistic interactions (Sutcliffe and Poole, 1978). In their study, and also in that by Stevenson and Poole (1976), this behavior might be more typical of established pairs, in which both members participate in territorial defense. This behavior, which requires a certain level of synchronism between the male and the female, could then be considered as a type of mutual investment between partners, which discourages desertion and reinforces the established bond. Simultaneous piloerection was practically absent in the pairs from NS group, while it was well-developed in pairs from RS group.

In our results, the duration of allogrooming by males and the frequency of simultaneous piloerection are the behavioral categories that present the major differences between the groups. These results suggest that females react differently to male behavior, which indicates their tendency to form stable bonds by participating in joint activities. The necessity for a greater level of investment by the male in order to stimulate female success in reproduction may have an adaptive value for females. This is

because the presence of the male and his participation in parental care directly influences the female's reproductive success (Ingram, 1977; Cleveland and Snowdon, 1984; Arruda *et al.*, 1986). This way, even indirect clues of this male's tendency could be detected by females, exerting influence on her reproductive physiology. It should be disadvantageous to females to begin ovulation, a reproductive attempt, without the male presence and continued cooperation.

In addition, the need of a high investment by the male for successful reproduction makes it disadvantageous for him to desert his mate and diminishes his availability to invest in relationships with other females.

Our results disagree with those of other studies that related the characteristics of interactions between males and females to reproductive success in pairs of *Callithrix jacchus* (Poole, 1978; Evans and Poole, 1983). However, they compared either pairs at different times of pairing, groups with different compositions, or different reproductive conditions of the pairs, e.g., groups in which the female was pregnant versus groups in which they were not and groups with and without newborn infants. More recent studies show that these factors could affect the expression of interactions between the partners (Rothe and Koenig, 1991; Mota *et al.*, 1995). On the other hand, our study is based on a more homogeneous sample: the subjects were all captive born and had no prior sexual experience, and the results were collected during a restricted time: the first 10 weeks after pairing. This could explain the differences obtained in our study.

Abbott *et al.* (1981; Abbott, 1984) demonstrated that the reproductive function of callitrichid females is influenced by social factors, as it occurs in subordinate females which undergo physiological inhibition by behavioral and physiological clues of dominant females. The reproductive condition of the females in the family group and the characteristics of the interactions with their mates might be considered factors associated with the rapidity of onset of reproductive function in RS females. The hypothesis of a reproductive effect caused by the behavioral interactions between the reproductive pair cannot be discarded, and it could be associated with the pair-bond relationship between males and females. However, more research is needed concerning the role of the pair-bond in each callitrichid species to understand better the causes of the unusual flexibility of their reproductive behavior.

ACKNOWLEDGMENTS

We thank Drs. Maria de Fátima Arruda and Maria Emília Yamamoto and two anonymous referees for their comments and suggestions, Sharon

Savage for help with the English, Antonio Barbosa da Silva for technical assistance with subject management, and the Departamento de Fisiologia of Universidade Federal do Rio Grande do Norte for the use of the monkeys from Núcleo de Primatologia. This research was supported by CNPq and FINEP.

REFERENCES

Abbott, D. H. (1984). Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. *Am. J. Primatol.* 6: 169-184.

Abbott, D. H., McNeilly, A. S., Lunn, S. F., Hulme, M. J., and Burden, F. J. (1981). Inhibition of ovarian function in subordinate female marmoset monkeys *Callithrix jacchus jacchus*). *J. Reprod. Fert.* 53: 335-345.

Arruda, M. F., Yamamoto, M. E., and Bueno, O. F. A. (1986). Interaction between parents and infants and infant–father separation in the common marmoset (*Callithrix jacchus*). *Primates* 27: 215-228.

Cleveland, J., and Snowdon, C. T. (1984). Social development during the first 20 weeks in the cotton-top tamarin (*Saguinus oedipus oedipus*). *Anim. Behav.* 32: 432-444.

Digby, L. J. (1994). *Social Organization and Reproductive Strategies in Wild Populations of Common Marmoset, Callithrix jacchus*, Doctoral thesis, University of California, Davis.

Epple, G. (1977). Notes on the establishment and maintenance of the pair-bond in *Saguinus fuscicollis*. In Kleiman, D. G. (ed.), *The Biology and Conservation of Callithrichidae*, Smithsonian Institution Press, Washington, DC, pp. 231-237.

Evans, S., and Poole, T. B. (1983). Pair-bond formation and breeding success in the common marmoset (*Callithrix jacchus jacchus*). *Int. J. Primatol.* 4: 83-97.

Ferrari, S. F., and Lopes Ferrari, M. A. (1989). A re-evaluation of the social organization of the Callithrichidae, with reference to the ecological differences between genera. *Folia Primatol.* 52: 132-147.

Hearn, J. P. (1978). The endocrinology of reproduction in the common marmoset, *Callithrix jacchus*. In: Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*, Smithsonian Institution Press, Washington, DC, pp. 163-171.

Hearn, J. P. (1983). The common marmoset (*Callithrix jacchus*). In Hearn, J. P. (ed.), *Reproduction in New World Monkeys*, MTP Press, Lancaster, pp. 181-215.

Hinde, R. A., and Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity as exemplified by mother–infant relations in rhesus monkeys. *Anim. Behav.* 18: 169-176.

Ingram, J. C. (1977). Interactions between parents and infants, and the development of independence in common marmoset (*Callithrix jacchus*). *Anim. Behav.* 25: 811-827.

Kendrick, K. M., and Dixson, A. F. (1983). The effect of ovarian cycle on the behavior of common marmosets (*Callithrix jacchus*). *Physiol. Behav.* 30: 735-742.

Kendrick, K. M., and Dixson, A. F. (1984). A quantitative description of copulatory and associate behaviors of captive marmosets (*Callithrix jacchus*). *Int. J. Primatol.* 5: 199-211.

Kleiman, D. G. (1977). Monogamy in mammals. *Q. Rev. Biol.* 52: 39-39.

Kleiman, D. G. (1978). Characteristics of reproduction and sociosexual interactions in pairs of lion tamarins (*Leontopithecus rosalia*) during the reproductive cycle. In Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*, Smithsonian Institution Press, Washington, DC, pp. 181-190.

Kuderling, I. (1990). Does the duration of living with the breeding pair influence the first reproductive success in *Saguinus fuscicollis* daughters? *Primate Report* 28: 19-24.

Mota, M. T. S., Sousa, M. B. C., and Campos, M. F. (1995). The effect of parturition on the interactions within pairs of common marmosets (*Callithrix jacchus*). *Braz. J. Med. Biol. Res.* 28: 108-112.

Poole, T. B. (1978). A behavioral investigation of "pair-bond" maintenance in *Callithrix jacchus jacchus*. In Rothe, H., Wolters, H. J., and Hearn, J. P. (eds.), *Biology and Behavior of Common Marmosets*, Eigenverlag, Gottingen, pp. 209-216.

Price, E. C. (1992). Sex and helping: Reproductive strategies of breeding male and female cotton-top tamarins, *Saguinus oedipus*. *Anim. Behav.* 43: 717-728.

Rothe, H. (1975). Some aspects of sexuality and reproduction in groups of captive marmosets (*Callithrix jacchus*). *Z. Tierpsy*, 35: 253-273.

Rothe, H., and Koenig, A. (1991). Variability of social organization in captive common marmosets (*Callithrix jacchus*). *Folia Primatol.* 57: 28-33.

Saltzman, W., Severin, J. M., Schultz-Darken, N. J., and Abbott, D. H. (1997a). Behavioral and social correlates os escape from suppression of ovulation in female common marmosets housed with the natal family. *Am. J. Primatol.* 41: 1-21.

Saltzman, W., Schultz-Darken, N. J., Severin, J. M., and Abbot, D. H. (1997b). Escape from social suppression of sexual behavior and of ovulation in female common marmosets. *Ann. N.Y. Acad. Sci.* (in press).

Savage, A., Ziegler, T. E., and Snowdon, C. T. (1988). Sociosexual development, pair bond formation, and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus oedipus*). *Am. J. Primatol.* 14: 345-359.

Siegel, S. (1975). *Estatística Não-Paramétrica Para as Ciências do Comportamento*, Editora McGraw-Hill do Brasil, São Paulo.

Snowdon, C. T. (1990). Mechanisms maintaining monogamy in monkeys. In Dewsbury, D. A. (ed.), *Contemporary Issues in Comparative Psychology*, L. Erlbaum, Sunderland, MA, pp. 225-251.

Soini, P. (1987). Sociosexual behavior of a free ranging *Cebuella Pygmaea* (Callithrichidae, Platyrrini): General behavioral repertoire. *Anim. Behav.* 24: 428-451.

Stevenson, M. F., and Poole, T. B. (1976). An ethogram of common marmoset (*Callithrix jacchus*): General behavioral repertoire. *Anim. Behav.* 24: 428-451.

Sutcliffe, A. G., and Poole, T. B. (1978). Scent marking and associate behaviors in captive common marmosets (*Callithrix jacchus jacchus*) with a description of the histology of scent glands. *J. Zool. Lond.* 185: 41-56.

Tardif, S. D., Carson, R. L., and Clapp, N. K. (1986). Breeding performance of captive-born cotton-top tamarin (*Saguinus oedipus*) females: Proposed explanations for colony differences. *Am. J. Primatol.* 11: 271-275 (1984).

Widowski, T. M., Ziegler, T. E., Elowson, A. M., and Snowdon, C. T. (1990). The role of males in the stimulation of reproductive function in female cotton-top tamarins, *Saguinus o. oedipus*. *Anim. Behav.* 40: 731-741.

Woodcock, A. J. (1982). The first weeks of cohabitation of newly-formed heterosexual pairs of common marmoset (*Callithrix jacchus*). *Folia Primatol.* 37: 228-254.

Ziegler, T. E., Epple, G., Snowdon, C. T., Porter, T. A., Belcher, A. M., and Kuderling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Anim. Behav.* 45:313-322.